

Functional coordination between branch hydraulic properties and leaf functional traits in miombo woodlands: implications for water stress management and species habitat preference

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Abstract We investigated functional coordination between branch hydraulic properties and leaf functional traits among nine miombo woodlands canopy tree species differing in habitat preference and phenology. Specifically, we were seeking to answer the question: are branch hydraulic properties coordinated with leaf functional traits linked to plant drought tolerance in seasonally dry tropical forests and what are the implications for species habitat preference? The hydraulic properties investigated in this study were stem area specific hydraulic conductivity (K_S), Huber value (H_V), and xylem cavitation vulnerability (Ψ_{50}). The leaf functional traits measured were specific leaf area (SLA), leaf dry matter content (LDMC), and mean leaf area (MLA). Generalists displayed significantly ($P < 0.05$) higher cavitation resistance (Ψ_{50}) and SLA, but lower sapwood specific hydraulic conductivity (K_S), leaf specific conductivity (K_L), MLA, and LDMC than mesic specialists. Although MLA was uncorrelated with Ψ_{50} , we found significant ($P < 0.05$) positive and negative correlations between plant hydraulic properties and leaf functional traits linked to plant drought tolerance ability,

indicating that the interactions between branch hydraulics and leaf functional traits related to plant drought tolerance ability may influence tree species habitat preference in water-limited ecosystems.

Keywords Huber value · Leaf dry matter content · Miombo woodlands · Specific leaf area · Stem area specific hydraulic conductivity · Xylem cavitation

Introduction

Miombo woodlands in southern Africa are a significant transitional biome situated between the mesic tropical rainforests and the arid savannas (Malaisse 1978). In this seasonally dry tropical forest, plant productivity and distribution are largely restricted by water stress (White 1983). As expected, the majority of canopy tree species display narrow habitat range, with distribution effectively confined to the relatively wet northern miombo woodlands (occurring above 1,000 mm mean annual precipitation). A few canopy species are widely distributed, occurring in both wet and dry miombo woodlands (Chidumayo 1987). The narrow habitat range species (mesic specialists) are brevi-deciduous, whereas the wide habitat range species (generalists) are drought-deciduous, suggesting that the two groups of species employ different mechanisms in dealing with water stress.

Given the intensity and severity of drought in this seasonally dry tropical forest (Frost 1996; Murphy and Lugo 1986), interactions between plant physiological and morphological traits may play a crucial role in explaining differences in species habitat specialization. In particular, interactions between branch hydraulic properties and leaf functional traits associated with drought tolerance may

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Table 1 The nine miombo woodland principal tree species studied

| Species | Genera | Leaf phenology | Functional group |
|---|-------------------------|-----------------|------------------|
| <i>Brachystegia boehmii</i> Benth | <i>Fabaceae</i> | Fully deciduous | Generalist |
| <i>Brachystegia longifolia</i> Benth | <i>Fabaceae</i> | Fully deciduous | Generalist |
| <i>Brachystegia spiciformis</i> Benth | <i>Fabaceae</i> | Fully deciduous | Generalist |
| <i>Erythrophleum africanum</i> (Benth.) Harms | <i>Fabaceae</i> | Fully deciduous | Generalist |
| <i>Pericopsis angolensis</i> (Baker) Meeuwen | <i>Fabaceae</i> | Fully deciduous | Generalist |
| <i>Brachystegia floribunda</i> Benth | <i>Fabaceae</i> | Brevi-deciduous | Mesic specialist |
| <i>Isoberlinia angolensis</i> (Benth.) Hoyle & Brenan | <i>Fabaceae</i> | Brevi-deciduous | Mesic specialist |
| <i>Julbernardia paniculata</i> (Benth.) Troupin | <i>Fabaceae</i> | Brevi-deciduous | Mesic specialist |
| <i>Marquesia macroura</i> Gilg | <i>Dipterocarpaceae</i> | Brevi-deciduous | Mesic specialist |

play a significant role in structuring such ecosystems (Reich et al. 1997). Separate pieces of evidence point in the direction of both branch hydraulic properties and leaf functional traits as reflecting a balance between plant water stress management and species ecological performance (Engelbrecht et al. 2000; Mencuccini 2003; Wright et al. 2002). Since the greatest impact of predicted climate change in seasonally dry tropical forests is likely to be in the magnitude and frequency of drought (IPCC 2007), understanding the relationships between branch hydraulic properties and leaf functional traits would add more insight into how these ecosystems will respond to future climate trends.

Comparative studies have shown that plant hydraulic conductivities tend to be higher under mesic sites than arid ones (Engelbrecht et al. 2000; Van der Willigen et al. 2000). Conversely, cavitation resistance (rapid phase change by xylem water under tension from liquid to vapour) has been observed to increase with increasing habitat aridity (Tyree and Zimmermann 2002). Consistent with these observations, it has been proposed that pressure for selection under arid environments favours plants with low hydraulic efficiency, but with high cavitation resistance (Canham et al. 2009; Zimmermann 1983). Ideally, this relationship suggests that plant hydraulic architecture has the potential to set species ecological boundaries by limiting hydraulically efficient individuals to the mesic habitats, while the less efficient but with secure xylems may compete in both mesic and arid habitats (Brodribb and Hill 1999; Lopez et al. 2005; Pockman and Sperry 2000).

Besides hydraulic response to drought, plants are also known to respond to water stress by modulating patterns of leaf carbon allocation (Niinemets 2001). For instance, it is a well-established fact that plants respond to water stress by modulating leaf size relative to leaf mass (Fonseca et al. 2000; Lamont et al. 2002; Reich et al. 1997). Available evidence also shows a trend towards smaller compact leaves, which are thicker and denser in arid environments than under mesic ones (Ackerly et al. 2002). Although

significant amount of evidence has coalesced in support of the hypotheses that both hydraulic properties and leaf functional traits are responsive to soil water variability, very little is known about the interactions between these two suites of traits for most dry tropical forests in Africa.

Therefore, the primary aims of this study were to evaluate the relationships between branch hydraulic properties and leaf functional traits associated with plant drought tolerance and to examine the extent to which these relationships influence species habitat preference. For examining these relationships, miombo woodlands, a seasonally dry tropical forest in southern Africa, was selected.

Materials and methods

Study site

In this study, two forest reserves with known forest management history were chosen to represent wet and dry miombo woodlands (White 1983). The two forest reserves experience summer rains, which occur between November and April followed by marked seasonal drought lasting from May to October. The wet site is Mwekera National Forest No. 6 located on the outskirts of City of Kitwe (12°49'S and 28°22'E; elevation of 1,295 m above sea level). The vegetation of the wet site is typically *Brachystegia-Julbernardia* woodlands with the genus *Brachystegia*, *Isoberlinia*, *Julbernardia*, and *Marquesia* as common canopy co-dominants (Chidumayo 1987). Average stand basal area and stand height are 39 m² ha⁻¹ and 21 m, respectively. The wet site receives an average annual precipitation of 1,200 mm with average annual temperatures ranging from 14 to 28°C. The dry site is Siamambo local forest, located in Choma District at 16°50'S and 27°03'E with an average elevation of 1,266 m above sea level. The vegetation of the dry site has *Brachystegia boehmii*, *Brachystegia spiciformis*, and *Julbernardia globiflora* as the common canopy co-dominants. Mean stand

Table 2 Summary of species leaf and stem hydraulic traits

| Site | Species | SLA (cm ² /g) | MLA (cm ²) | LDMC (g g ⁻¹) × 10 ⁻² | Ψ ₅₀ (MPa) | K _S (kg s ⁻¹ MPa ⁻¹ m ⁻¹) | H _v | K _L (kg s ⁻¹ MPa ⁻¹ m ⁻¹) × 10 ⁻⁴ |
|------|-----------------------|-----------------------------|---------------------------|---|-----------------------|---|----------------|--|
| Wet | <i>B. boehmii</i> | 433 ± 14 | 30 ± 1 | 8.1 ± 0.4 | -3.2 ± 0.11 | 5.74 ± 0.3 | 2.9 ± 0.02 | 1.66 ± 0.12 |
| | <i>B. longifolia</i> | 470 ± 13 | 27 ± 2 | 8.6 ± 0.3 | -2.5 ± 0.08 | 5.17 ± 0.3 | 2.8 ± 0.02 | 1.41 ± 0.12 |
| | <i>B. spiciformis</i> | 522 ± 15 | 89 ± 4 | 7.8 ± 0.3 | -2.8 ± 0.08 | 7.47 ± 0.5 | 2.3 ± 0.02 | 1.71 ± 0.15 |
| | <i>E. africanum</i> | 562 ± 34 | 33 ± 1 | 6.6 ± 0.6 | -3.1 ± 0.09 | 9.97 ± 0.4 | 2.0 ± 0.01 | 1.98 ± 0.15 |
| | <i>P. angolensis</i> | 504 ± 18 | 73 ± 3 | 6.3 ± 0.3 | -3.2 ± 0.10 | 9.43 ± 0.4 | 2.4 ± 0.02 | 2.27 ± 0.22 |
| | <i>B. floribunda</i> | 488 ± 43 | 112 ± 4 | 11.3 ± 1 | -1.7 ± 0.20 | 13.73 ± 0.6 | 2.4 ± 0.01 | 3.32 ± 0.27 |
| | <i>I. angolensis</i> | 383 ± 13 | 202 ± 8 | 12.1 ± 0.5 | -2.0 ± 0.22 | 24.19 ± 1.3 | 2.8 ± 0.01 | 6.86 ± 0.05 |
| | <i>J. paniculata</i> | 403 ± 12 | 157 ± 6 | 13.6 ± 0.6 | -2.2 ± 0.10 | 15.58 ± 0.9 | 2.1 ± 0.01 | 3.33 ± 0.24 |
| | <i>M. macroura</i> | 418 ± 13 | 122 ± 4 | 11.3 ± 0.4 | -1.5 ± 0.34 | 21.07 ± 0.8 | 2.5 ± 0.02 | 5.32 ± 0.44 |
| Dry | <i>B. boehmii</i> | 629 ± 42 | 24 ± 0.8 | 7.2 ± 0.5 | -3.6 ± 0.14 | 2.77 ± 0.07 | 2.2 ± 0.1 | 0.59 ± 0.03 |
| | <i>B. spiciformis</i> | 620 ± 14 | 44 ± 1 | 7.0 ± 0.3 | -3.6 ± 0.12 | 5.33 ± 0.18 | 1.4 ± 0.1 | 0.7 ± 0.04 |
| | <i>E. africanum</i> | 474 ± 8 | 32 ± 0.7 | 7.4 ± 0.5 | -3.0 ± 0.10 | 8.19 ± 0.28 | 2.1 ± 0.2 | 1.59 ± 0.09 |
| | <i>P. angolensis</i> | 562 ± 18 | 57 ± 2 | 7.0 ± 0.5 | -2.8 ± 0.13 | 10.53 ± 0.35 | 2.2 ± 0.1 | 2.21 ± 0.1 |

Standard errors of the mean are at 95% confidence interval

SLA specific leaf area, MLA mean leaf area, LDMC leaf dry matter content, Ψ₅₀ cavitation resistance at 50% loss in conductivity, K_S specific leaf conductivity, H_v Huber value, K_L leaf specific conductivity

basal area and stand height are 14 m² ha⁻¹ and 15 m, respectively. The dry site receives 800 mm of mean annual precipitation with mean annual temperatures ranging between 12 and 27°C.

Sampling

To examine the relationship between branch hydraulic properties and leaf functional traits, nine miombo woodlands canopy tree species were selected (Table 1).

The nine canopy tree species were selected on the basis that: (1) they differed substantially in habitat preference (Chidumayo 1987; Smith and Allen 2004), (2) they had contrasting leaf phenology, (3) there was no substantial taxonomical difference between them and, (4) they formed much of the canopy throughout the miombo woodlands. We sampled 25 GPS-referenced trees per species (giving a total of 225 trees at the wet site and 100 trees at the dry site). Generalists were sampled on both the wet and dry sites. Mesic specialists were only sampled on the wet site. Leaf measurements were carried out in June 2007 and April to June 2008. Data collection coincided with the end of the rainy season, by which time the leaves had reached full maturity and the soils were still well hydrated.

Leaf measurements

Three leaf-bearing, light-exposed branches were harvested per tree (between 0530 and 0730 hours local time) and quickly wrapped in wet towels. The samples were always placed in opaque plastic bags to ensure that leaves

remained well hydrated. The full procedures for specific leaf area (SLA) and leaf dry matter content (LDMC) determination followed those of Westoby (1998) and Garnier et al. (2001). At the laboratory, one healthy and fully expanded leaf was harvested from each branch. The main criteria for selecting a leaf for measurement were that it had not suffered any leaf blade damage, was mature (hardened leaf blade), and actively photosynthesizing (green in colour). Prior to scanning (using Flatbed scanner—Packard Bell Diamond 1200 Plus, Packard Bell, UK) the leaves were initially weighed to get wet weight. The scanned leaves were then oven-dried at a constant temperature of 72°C for 48 h to a constant oven-dry weight (Ackerly et al. 2002; Sellin and Kupper 2006; Westoby and Wright 2003).

Leaf areas for the scanned images were determined using the software Image J (freely available from <http://rsb.info.nih.gov/ij/>). SLA (cm² g⁻¹) was calculated as the ratio of leaf area to its oven-dry mass. LDMC (g g⁻¹) was calculated as the ratio of leaf oven-dry weight to its wet weight.

Hydraulic properties measurement

Xylem hydraulic conductivity was measured on morphologically identical leaf-bearing branches (Patino et al. 1995). The branches were harvested in the early hours of the morning (between 0530 and 0830 hours). The under-bark diameter for the harvested twigs ranged from 4 to 10 mm. The harvested branches were always covered with wet towels and sealed in dark plastic sample bags to

Table 3 Results of linear mixed effects analysis of variance for co-occurring generalists and mesic specialists in wet and dry miombo woodland sites

| Variable | Source | df | MS | F ratio | P value | VC |
|---|--------------------------------------|-----|---------|---------|---------|-------|
| SLA (g cm ⁻²) | Functional type | 1 | 1.0602 | 12.68 | 0.009 | 7.53 |
| | Species (functional type) | 7 | 0.0836 | 2.96 | 0.006 | 4.16 |
| | Individual (functional type species) | 216 | 0.0282 | 2.01 | <0.001 | 43.35 |
| LDMC (g g ⁻¹) | Functional type | 1 | 1.9077 | 48.08 | <0.001 | 28.67 |
| | Species (functional type) | 7 | 0.0396 | 3.65 | 0.001 | 4.17 |
| | Individual (functional type species) | 216 | 0.0108 | 2.31 | <0.001 | 35.30 |
| MLA (cm ²) | Functional type | 1 | 43.3102 | 14.32 | 0.007 | 54.55 |
| | Species (functional type) | 7 | 3.0239 | 65.68 | <0.001 | 26.66 |
| | Individual (functional type species) | 216 | 0.0460 | 4.17 | <0.001 | 12.53 |
| K_S (kg s ⁻¹ MPa ⁻¹ m ⁻¹) | Functional type | 1 | 25.4633 | 661.33 | <0.001 | 49.72 |
| | Species (functional type) | 7 | 1.1288 | 29.32 | <0.001 | 15.43 |
| | Individual (functional type species) | 216 | 0.0385 | 1.82 | <0.001 | 16.24 |
| H_v | Functional type | 1 | 0.0125 | 0.66 | 0.417 | 0.14 |
| | Species (functional type) | 7 | 0.0678 | 3.58 | 0.001 | 5.40 |
| | Individual (functional type species) | 216 | 0.0189 | 2.02 | <0.001 | 46.52 |
| K_L (kg s ⁻¹ MPa ⁻¹ m ⁻¹) | Functional type | 1 | 6.9027 | 234.3 | <0.001 | 32.07 |
| | Species (functional type) | 7 | 0.2375 | 8.06 | <0.001 | 7.72 |
| | Individual (functional type species) | 216 | 0.0294 | 2.01 | <0.001 | 29.57 |
| Ψ_{50} (MPa) | Functional type | 1 | 65.3256 | 12.18 | 0.01 | 7.63 |
| | Species (functional type) | 7 | 5.3625 | 3.10 | 0.004 | 4.18 |
| | Individual (functional type species) | 216 | 1.7298 | 1.84 | <0.001 | 41.58 |

K_S stem area specific hydraulic conductivity, H_v Huber value, K_L leaf specific conductivity, SLA specific leaf area, MLA mean leaf area, $LDMC$ leaf dry matter content, MS mean square, VC variance component

minimize transpiration and emboli development. At the laboratory, the segments were trimmed to approximately equal length as the determined species maximum vessel length plus 10% allowance in order to avoid open vessels (Vinya et al. unpublished). Throughout the process of sample preparation, segments were always kept wholly immersed in water. Prior to hydraulic determination, segments were flushed with distilled water at a constant pressure of 150 kPa for periods ranging from 20 to 30 min depending on species and extent of xylem embolism. Hydraulic conductivity was gravimetrically determined by inserting the basal end of the trimmed twig into a custom-built water reservoir with a low delivery pressure head of 2 kPa. Maximum hydraulic conductivity was determined by forcing degassed, filtered (to 0.2 μ m) and acidified (with HCl, pH 2) distilled water through the segments (Kolb et al. 1996; Sperry et al. 1988). Each segment was allowed to equilibrate for 30 min before initial flow rate was measured. Sap flow was measured by attaching a pre-weighed cotton wool onto the free distal end of the segment. At the end of each flow determination, segment underbark diameter and length were accurately measured. Maximum hydraulic conductivity (K_H) was calculated as:

$$K_H = \left(\frac{J_v}{(\Delta P/l)} \right) (\text{Kg} \cdot \text{s}^{-1} \text{MPa}^{-1} \text{m}) \quad (1)$$

Where K_H is the maximum hydraulic conductivity, J_v is the flow rate (kg s⁻¹), ΔP is the delivery pressure (MPa), and l is segment length (m).

Stem area sapwood specific conductivity (K_S , kg s⁻¹ m⁻¹ MPa⁻¹) was derived by dividing hydraulic conductivity with the effective sapwood cross-sectional area (A_w , m²).

Huber value (H_v ; cm² cm⁻²) was calculated as the ratio of the sapwood cross-sectional area to the total supported leaf area:

$$H_v = \frac{A_w}{A_L} \quad (2)$$

where A_L (m²) is the total leaf area supported by the twig.

Determination of xylem vulnerability to cavitation

We used the standard laboratory bench air-drying technique to induce cavitation in branches (Cochard et al. 1992). Branches were progressively dehydrated to various water potentials over a period of 6–48 h depending on

Table 4 Results of two-way ANOVA comparing wet and dry miombo woodland sites generalists

| | Scale | df | MS | F ratio | P value | VC |
|--|-------------|-----|--------|---------|---------|------|
| SLA (g cm ⁻²) | Site | 1 | 0.142 | 18.7 | <0.001 | 7.3 |
| | Species | 3 | 0.026 | 3.4 | 0.019 | 4 |
| | Interaction | 3 | 0.090 | 11.83 | <0.001 | 13.8 |
| | Error | 192 | 0.007 | | | 75 |
| LDMC (g g ⁻¹) | Site | 1 | 0.0004 | 0.08 | 0.77 | 0.04 |
| | Species | 3 | 0.014 | 2.89 | 0.036 | 4.2 |
| | Interaction | 3 | 0.0117 | 2.41 | 0.068 | 3.5 |
| | Error | 192 | 0.0048 | | | 92.3 |
| MLA (cm ²) | Site | 1 | 0.829 | 69.08 | <0.001 | 8.7 |
| | Species | 3 | 1.926 | 160.46 | <0.001 | 60.8 |
| | Interaction | 3 | 0.198 | 16.5 | <0.001 | 6.3 |
| | Error | 192 | 0.012 | | | 24 |
| <i>H_v</i> | Site | 1 | 0.0823 | 12.05 | 0.001 | 5 |
| | Species | 3 | 0.055 | 8.06 | <0.001 | 10 |
| | Interaction | 3 | 0.035 | 5.16 | 0.002 | 6 |
| | Error | 192 | 0.007 | | | 79 |
| <i>K_S</i> (kg s ⁻¹ MPa ⁻¹ m ⁻¹) | Species | 3 | 1.6 | 197.84 | <0.001 | 60 |
| | Site | 1 | 0.738 | 91.29 | <0.001 | 9.3 |
| | Interaction | 3 | 0.279 | 34.5 | <0.001 | 11 |
| | Error | 192 | 0.008 | | | 20 |
| <i>K_L</i> (kg s ⁻¹ MPa ⁻¹ m ⁻¹) | Species | 3 | 0.358 | 47.16 | <0.001 | 30 |
| | Site | 1 | 0.586 | 77.21 | <0.001 | 16 |
| | Interaction | 3 | 0.160 | 21.11 | <0.001 | 13 |
| | Error | 192 | 0.0076 | | | 40 |
| Ψ_{50} (MPa) | Species | 3 | 0.0193 | 0.41 | 0.74 | 0.62 |
| | Site | 1 | 0.0043 | 0.09 | 0.76 | 0.05 |
| | Interaction | 3 | 0.081 | 1.73 | 0.16 | 2.6 |
| | Error | 192 | 0.047 | | | 97 |

SLA specific leaf area, MLA mean leaf area, LDMC leaf dry matter content, Ψ_{50} cavitation resistance at 50% loss in conductivity, *K_S* specific leaf conductivity, *H_v*, Huber value, *K_L* leaf specific conductivity

species. We dehydrated the branches to varying range of water potentials corresponding to 0 to >80% loss of hydraulic conductance. Prior to water potential determination, small distal segments were excised from the main twig and placed in airtight plastic bags for 30 min to allow for water potential equilibration. This was then followed by water potential determination (Ψ) using a pressure chamber (SKPM 1405, Skye Instruments Ltd, UK).

For construction of vulnerability curves, hydraulic conductivity (*K_{Hmin}*) was initially determined on dehydrated segments using the gravimetric technique. This was followed by flushing out emboli as described above and re-measurement of *K_H* to obtain *K_{Hmax}*. Percent reduction in hydraulic conductivity (PLC) was then calculated as:

$$PLC = \frac{K_{Hmax} - K_{Hmin}}{K_{Hmax}} \times 100 \quad (3)$$

where *K_{Hmax}* is the maximum hydraulic conductivity without emboli and; *K_{Hmin}* is initial hydraulic

conductivity with emboli. To confirm that the segments had thoroughly been freed of emboli, they were perfused with Safranin dye at the end of each experiment. Vulnerability curves were fitted with the following sigmoid function:

$$PLC = 100 / (1 + \exp(a(\Psi - \Psi_{50}))) \quad (4)$$

where Ψ_{50} is the water potential causing 50% reduction in hydraulic conductance, and *a* represents the slope of the vulnerability curve (Pammenter and Van der Willigen 1998).

Statistics

Differences between functional groups (generalists vs. specialists) were analysed using a linear mixed-effects model ANOVA (Zar 2010). We used a two-way ANOVA to test for the effects of site and species (Hofmann and

Franco 2003). Intra-species differences between wet and dry site generalists were analysed using two-sample *t* tests. We used linear regression analysis to determine the relationship between hydraulic properties and leaf functional traits. Data were log transformed because these failed both the normality and constant variance tests. Huber value data were arcsine transformed prior to log transformation, because these were in proportion format. All statistical analyses were performed in Minitab (Version 15, Minitab Inc., PA, USA).

Results

Hydraulic properties and leaf functional traits

There were significant ($P < 0.05$) differences in the range of branch hydraulic properties and leaf functional traits measured for the principal miombo woodland tree species in this study (Table 2).

We observed significant ($P < 0.05$) variations in both hydraulic properties and leaf functional traits between the two miombo woodlands functional groups (generalists versus mesic specialists) examined in this study (Table 3).

However, Huber value (H_v) did not vary significantly ($P > 0.05$) between the two miombo woodlands functional groups.

Shift in hydraulic and leaf functional traits between wet and dry miombo woodlands

Across generalist populations, LDMC and Ψ_{50} varied insignificantly ($P > 0.05$) over the examined spatial scale (Table 4).

By contrast, K_S , K_L , MLA, and H_v varied significantly ($P < 0.05$) between the examined sites in this study (Table 4).

At the intra-species level, there were significant ($P < 0.05$) reductions in K_S from wet to dry miombo woodland sites for three (*B. boehmii*, *B. spiciformis*, and *Erythrophleum africanum*) out of the four generalists (Fig. 1).

Among the four generalists, only *B. spiciformis* showed a significant (two-sample *t* test assuming equal variances, $P = 0.006$) intra-species increase in cavitation resistance from wet to dry site. However, for the other three generalists (*B. boehmii*, *E. africanum* and *P. angolensis*) examined in this study, we observed an insignificant ($P > 0.05$) intra-species differences in Ψ_{50} between wet and dry sites.

Brachystegia boehmii, *B. spiciformis*, and *P. angolensis* showed a trend of increasing SLA from wet to dry site, with *E. africanum* being the only generalist species showing the opposite trend (Figs. 1, 2). LDMC followed a

similar trend as SLA from wet to dry miombo woodland sites for the four generalists. As expected, MLA showed a declining trend from wet to dry miombo woodland site in *B. boehmii*, *B. spiciformis*, and *P. angolensis*.

Relationships between branch hydraulics and leaf functional traits

Across species, sapwood specific hydraulic conductivity (K_S) was negatively correlated to SLA ($r = 0.76$, $P = 0.02$), but positively correlated to both LDMC ($r = 0.74$, $P < 0.02$) and MLA ($r = 0.90$, $P = 0.001$). A linear regression analysis explained 58, 54, and 82% of the variability in SLA, LDMC, and MLA, respectively (Fig. 3).

There was a significant ($r = 0.75$, $P = 0.02$) negative correlation between Ψ_{50} and SLA. Ψ_{50} was, however, significantly and positively correlated to LDMC ($r = 0.79$, $P = 0.01$). On the contrary, Ψ_{50} was not correlated to MLA ($r = -0.56$, $P = 0.12$). A linear regression explained 56, 63, and 31% of the variability in SLA, LDMC, and MLA, respectively (Fig. 4).

However, Huber value was not correlated to any of the three leaf functional traits (SLA, LDMC, and MLA).

Discussion

As expected, miombo woodland tree species with wide habitat selection (generalists) converged towards high cavitation resistance, low hydraulic efficiency, and high SLA, but low LDMC and mean leaf area (MLA) (Table 2). By comparison, mesic specialists exhibited high hydraulic efficiency, but are more vulnerable to xylem cavitation with low SLA but high LDMC and MLA. Our findings on plant hydraulic properties are consistent with other studies (Brodrigg and Hill 1999; Pockman and Sperry 2000).

It has been proposed that pressure for selection under arid environments favour plants with low SLA (Fonseca et al. 2000) and high cavitation resistance (Tyree and Zimmermann 2002). Consistent with these observations, one expects a positive relationship between SLA with Ψ_{50} . By contrast, our results showed a negative association between SLA with both Ψ_{50} and K_S , (Figs. 3, 4) indicating that species with low leaf mass per area were more resistant to drought-induced xylem cavitation than ones with high leaf mass per area. The most plausible explanation for the seemingly contradictory result may be attributed to the differences in leaf phenology between the two miombo woodlands functional groups. Several pieces of evidence point in the direction of leaf construction costs and leaf life span being negatively correlated with SLA (Eamus et al. 1999; Kikuzawa 1995; Sabrado 1991; Villar and Merino

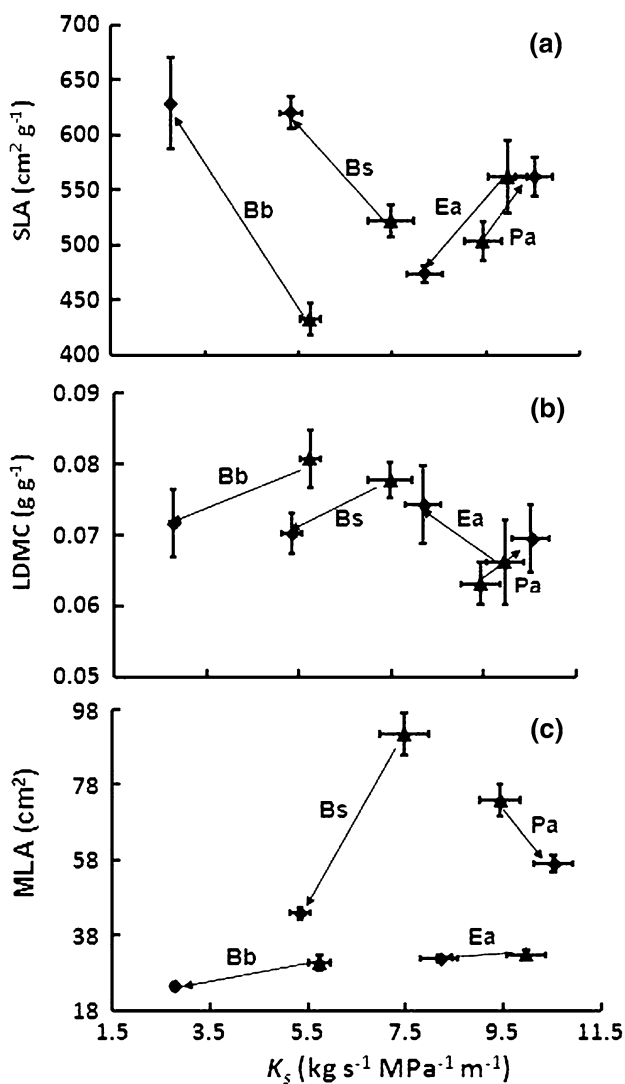


Fig. 1 Shifts in specific hydraulic conductivity and leaf functional traits between wet and dry miombo woodland habitats: **a** specific leaf area (SLA); **b** leaf dry matter content (LDMC); **c** mean leaf area (MLA). Chart symbols are: *arrows* represent trait shift from wet to dry miombo woodland sites

2001). In the case of this seasonally dry tropical forest, the drought-tolerant miombo woodlands generalist tree species are fully deciduous, whereas mesic specialists are characteristically brevi-deciduous (Table 1). Thus, in terms of leaf carbon economics, it is cheaper for the fully deciduous generalists to support leaves with low SLA because of the presumably low construction costs. It is, therefore, not surprising that in this seasonally dry tropical forest, there is a pronounced trend towards low SLA and high cavitation resistance from wet to dry sites (Fig. 2).

LDMC has often been linked to leaf adaption to withstand desiccation, such that high LDMC leaves are thicker and stiffer than low ones (Groom and Lamont 1997). As expected, plants adapted to arid habitats tend to develop

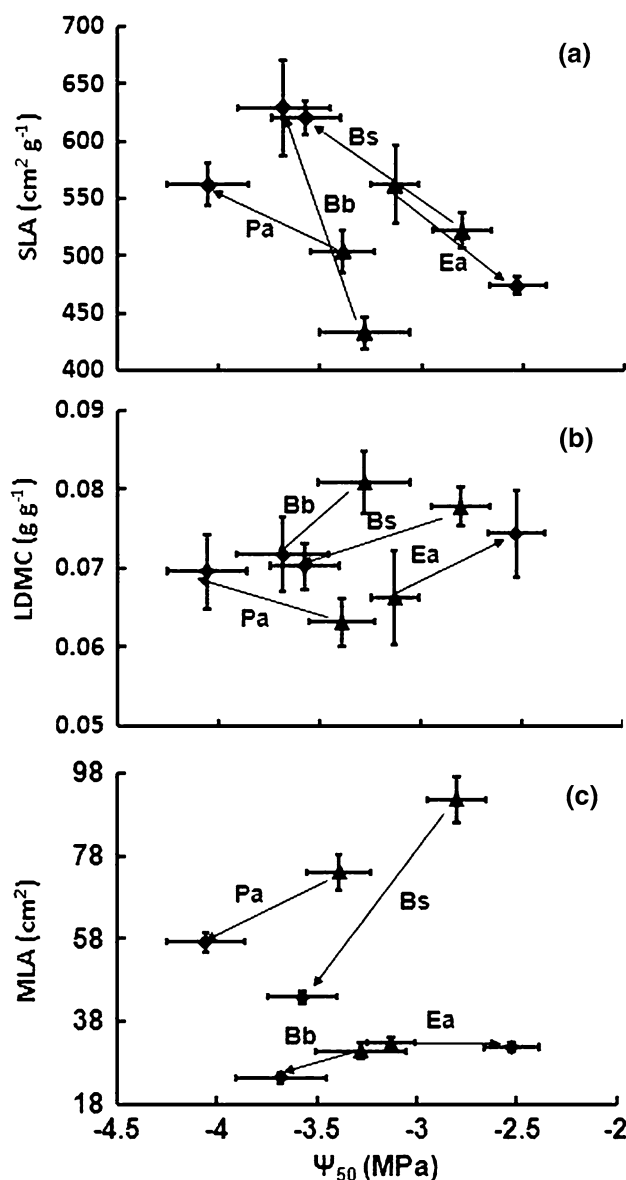


Fig. 2 Shifts in xylem vulnerability to cavitation and leaf functional traits between wet and dry miombo woodland habitats: **a** specific leaf area (SLA); **b** leaf dry matter content (LDMC); **c** mean leaf area (MLA). Chart symbols are: *arrows* represent trait shift from wet to dry miombo woodland sites

leaves high in LDMC and those from mesic habitats display an opposite trend. Thus, LDMC has repeatedly been viewed as a good predictor of plant ecological strategy (Wilson et al. 1999). Ideally, the general hypotheses, which propose a convergence towards increased cavitation resistance and high LDMC under arid environments, expect an inverse relationship between LDMC and Ψ_{50} and K_s . Surprisingly, we found an opposite pattern in which LDMC was positively associated with both Ψ_{50} and K_s (Figs. 3, 4).

A positive relationship between LDMC and Ψ_{50} in this study arose due to differences in leaf phenology between

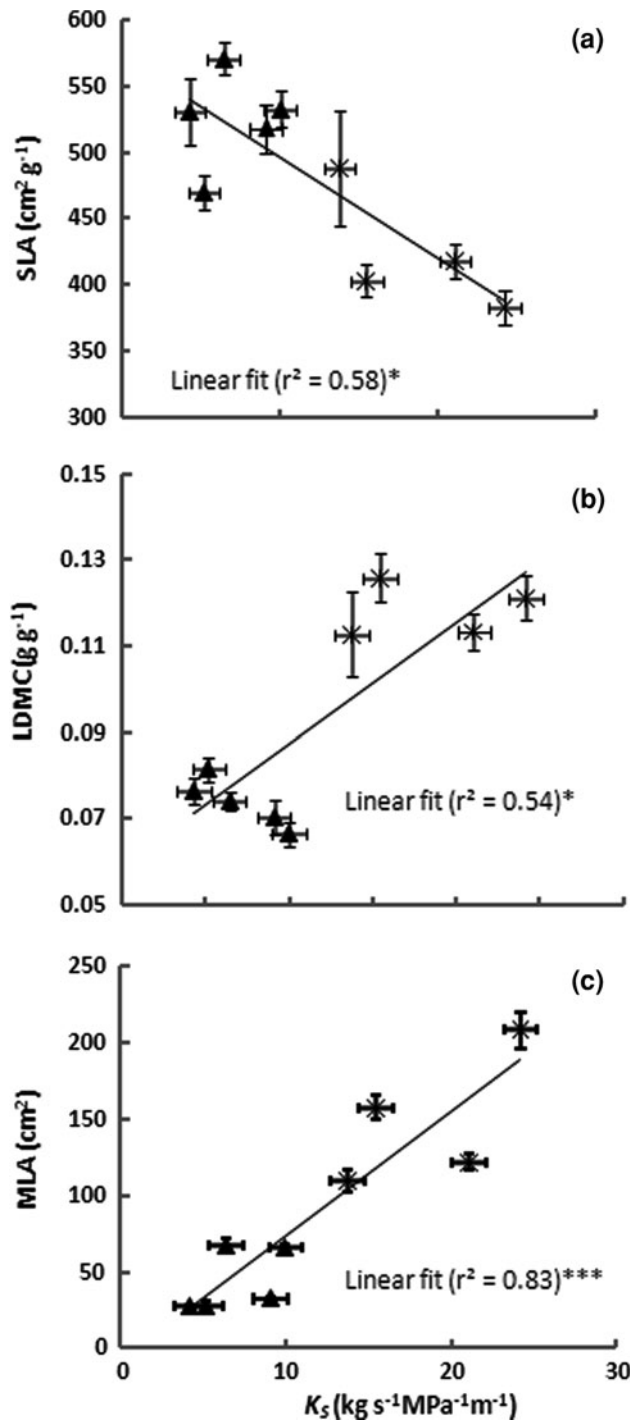


Fig. 3 Relationship between stem area specific hydraulic conductivity (K_s) and leaf functional traits: **a** specific leaf area (SLA); **b** leaf dry matter content (LDMC); **c** mean leaf area (MLA). Regression line data points are tree species mean \pm SE ($n = 25$ trees per species). The fitted lines for graphs **a**, **b** and **c**, respectively, have the equations: $y = 2.83 - 0.17\chi$ ($F = 9.69$, $P = 0.017$); $y = 1.07 + 0.16\chi$ ($F = 8.37$, $P = 0.023$) and; $y = 0.71 + 1.13\chi$ ($F = 31.36$, $P = 0.001$). Chart symbols are: *closed triangles* generalists, *multi symbols* mesic specialists, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$, *ns* not significant

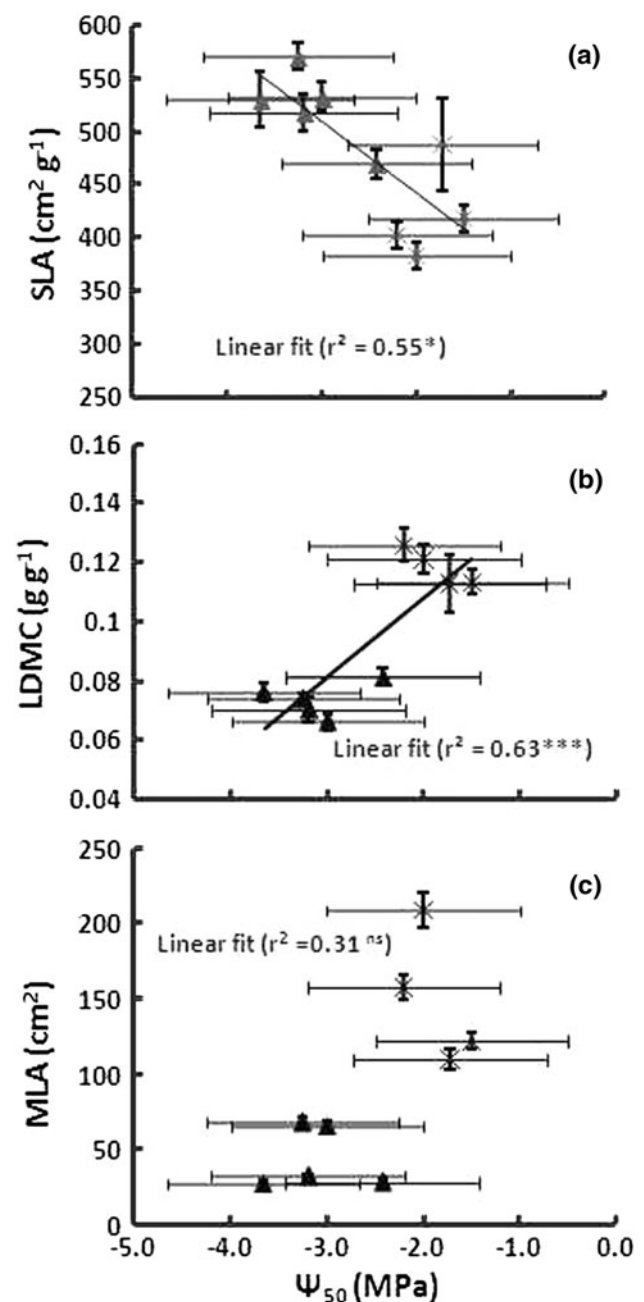


Fig. 4 Relationship between xylem vulnerability to cavitation and leaf functional traits: **a** specific leaf area (SLA); **b** leaf dry matter content (LDMC); **c** mean leaf area (MLA). Regression line data points are tree species mean \pm SE ($n = 25$ trees per species). Regression models describing the relationships are: $y = 2.54 - 0.053\chi$ ($F = 8.72$, $P = 0.021$); $y = 1.37 + 0.057\chi$ ($F = 11.87$, $P = 0.011$); and $y = 2.38 + 0.23\chi$ ($F = 3.18$, $P = 0.118$). Chart symbols are: *closed triangles* generalists, *multi symbols* mesic specialists, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$, *ns* $P > 0.05$

the two miombo woodlands functional groups. Firstly, high LDMC leaves are generally expensive to construct as they entail greater leaf carbon investment to reinforce desiccation resistance (Williams et al. 1989). Secondly, numerous

studies have suggested that high LDMC confers the ability to plants to withstand lower negative leaf water potentials, hence enabling such species to maintain physiological processes under drought conditions (Kursar et al. 2009; Oertli et al. 1990; Zimmermann 1978). We believe that a combination of high LDMC with an efficient hydraulic architecture allows the low cavitation resistant mesic specialists to be physiologically active throughout the year. The net benefit of being productive throughout the year is the increased carbon investment in the photosynthetic apparatus, which gives rise to increased foliar carbon investment. On the other hand, low LDMC among the fully deciduous miombo woodlands generalists results in low desiccation resistance and as such these respond to seasonal drought by shedding leaves. Therefore, ability to limit seasonal water losses through leaf shedding, coupled with a xylem structure that is resistant to cavitation, enables miombo generalists to be successful in both the mesic and arid miombo woodland habitats.

Across species, we did not find a significant association between Ψ_{50} and MLA suggesting that these two traits are not functionally coordinated in this water-limited tropical forest. The advantages of small leaves under arid environments have been emphasized in a number of studies. For instance, it has been suggested that small leaves are better adapted to minimize leaf overheating under drought-prone environments than large ones (Parkhurst and Loucks 1972). Therefore, the lack of correlation between Ψ_{50} and MLA is quite surprising given the tight relationship between leaf size and transpiration rate (Hopkins and Hüner 2009). Interesting enough, K_S was strongly associated with MLA suggesting the existence of a physiological link between average leaf size and hydraulic efficiency. This is consistent with numerous studies that have demonstrated a positive relationship between hydraulic efficiency and stomatal conductance (Brodribb et al. 2002; Hubbard et al. 2001). As expected in this seasonally dry tropical forest, both hydraulic efficiency and MLA demonstrated significant reductions from wet to dry habitats, suggesting a significant shift towards reductions in plant water losses under arid habitats.

Conclusions

This study has demonstrated that differences in habitat preference between the two miombo woodland functional groups are as a result of variations in plant hydraulic properties as well as leaf functional traits. Tree species with wide habitat occurrences have xylem structures that are more resistant to cavitation than narrow habitat range of mesic specialists. Furthermore, generalists display high SLA, but low LDMC and MLA in comparison to mesic

specialists. These results suggest that the interaction between plant hydraulic properties and leaf functional traits may exert some influence on the range of habitats that any given tree species can successfully colonize in seasonally dry tropical forests.

Authors contribution Royd Vinya designed, collected, and analysed field data. Yadvinder Malhi, Nick Brown, and Joshua B. Fisher helped with the research design and statistical analysis.

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